MORPHOLOGY OF THE HEAD OF TRICHOPTEROUS LARVÆ AS A BASIS FOR THE REVISION OF THE FAMILY RELATIONSHIPS.[1]

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Introduction.

The general and detailed anatomy of trichopterous larvæ has been thoroughly dealt with by several well-known investigators. A study of the sclerites of the head has led the author to a reconsideration of the phylogeny within the group, and the conclusions reached by him seem to warrant this addition to the literature.

The generally accepted classification of the Trichoptera gives as the stem form the family Rhyacophilidæ. The Hydroptilidæ or microtrichopterans are considered an early offshoot as are also the Philopotamidæ. In the same way the Psychomyidæ, Polycentropidæ and Hydropsychidæ possess certain relationships. These six families constitute a major subgroup. The remaining seven families make up a second subgroup. They are the Calomoceratidæ and Odontoceridæ; the Leptoceridæ and Molannidæ; the Phryganeidæ, Limnophilidæ and the Sericostomatidæ. The family relationships are as suggested here although the last family is made up of four subfamilies of somewhat doubtful affiliations.

The first subgroup has thysanuriform or campodeiform larvæ; the last group has eruciform larvæ. The outcome of the present study indicates that the stem form is to be found not in the campodeiform group, but rather in the eruciform group, namely the Leptoceridæ; and that the campodeiform is a specialized rather than a primitive condition among trichopterous larvæ.

Acknowledgments.

The present study had its origin in a problem undertaken at the suggestion of Dr. Cornelius Betten in 1913. The results were pub-

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[1] Contributions from the Entomological Laboratories of the University of Illinois, No. 68. The publication of this paper has been made possible through an appropriation for plates by the University of Georgia, D. C. Barrow Chancellor.

lished at that time in the form of a key to Trichopterous larvæ (Krafka, 1915). The possibility of the relationships as herein indicated was first suggested to the author by Dr. Alex. D. MacGillivray, and the work has progressed under his direction.

The Illinois State Laboratory of Natural History has kindly loaned material some of which has proved exceptionally valuable. The greater part of the material comes from the private collection of Dr. Betten. The nature of my indebtedness to him is rather unusual. At his suggestion I first undertook the study of the trichopterous larvæ. These studies have led to conclusions seemingly opposed to his own. Yet his criticism has been generously given and he has lent assistance in every way possible to facilitate the successful outcome of the studies.

All heads described are figured. The explanation of the plates gives the source of the specimens.

CAMPODEIFORM AND ERUCIFORM LARVÆ.

1. *General Meaning and Significance:* The campodeiform (thysanuriform) and eruciform types of larvæ have been recognized in many orders of insects as respectively generalized and specialized in their organization. Folsom in his textbook of Entomology differentiates them as follows: "The former term is applied to many larvæ and nymphs on account of their resemblance to the Thysanura." "The resemblance lies chiefly in the flattened form, hard plates, long legs and antennæ, caudal cerci, well-developed mandibulate mouth-parts and active habits with the accompanying sensory specialization. These characteristics are permanent in Thysanura, but only temporary in metamorphic insects, and their occurrence in the latter forms may properly be taken to indicate that these insects have been derived from ancestors which were like Thysanura.

"These primitive characters are gradually overpowered in course of larval evolution, by secondary, or adaptive features.

"The prevalent type of larvæ among holometabolous insects is the eruciform, illustrated by a caterpillar or maggot. Here the body is cylindrical and often fleshy, the integument weak; the legs, antennæ, cerci and mouthparts reduced often to disappearance; the habits sedentary and the sense organs correspondingly reduced.

"The eruciform is clearly derived from the thysanuriform type as

Brauer and Packard have shown; the continuity of the two types being established by a complete series of intermediate stages."

2. *Occurrence in Trichoptera:* The two types of larvæ have long been recognized in the Trichoptera. The chief characteristics of each group may best be listed as opposites.

CAMPODEIFORM.	ERUCIFORM.
1. Long axis of the head continuous with long axis of the body.	1. Long axis of the head at right angles with the long axis of the body.
2. Mouth directed cephalad.	2. Mouth directed ventrad.
3. Body depressed.	3. Body cylindrical.
4. Legs long, generally all about same length.	4. Front legs much shorter than other two pairs.
5. Abdominal segments sharply constricted.	5. Abdominal segments faintly indicated.
6. Prolegs long, slender, and movable.	6. Prolegs short, thick, and fixed.
7. Lateral line wanting.	7. Lateral line generally present.
8. Prosternal horn wanting.	8. Prosternal horn sometimes present.
9. Abdominal tubercles wanting.	9. Abdominal tubercles usually present.
10. Rectal blood gills generally present.	10. Rectal blood gills wanting except in Leptoceridæ.
11. Free living, net builders, except Hydroptilidæ.	11. Building portable cases.

The characteristics peculiar to the campodeiform larvæ in the Trichoptera are those distinguishing the campodeiform larvæ of other orders of insects, while the same is true for the eruciform. Furthermore the various structures of the body may be arranged in an intergrading series consistent with the idea that the eruciform type is derived from the campodeiform.

This hypothesis is given additional support by the relationships as established among the adults. The Rhyacophilidæ have been taken as the stem form, since some members of this family retain the venation of the hypothetical wing type of Comstock. Furthermore those families which are placed nearest the Rhyacophilidæ on the basis of wing venation are characterized by campodeiform larvæ.

These three facts would seem to establish beyond a doubt the relationship within the order, at least as far as the two main groups are concerned.

MORPHOLOGY OF THE HEAD.

1. *Methods of Study:* While the study of insect anatomy entails no special technique, it is well in an investigation of this type to give the principal steps in the method used.

The larvæ were preserved in 75 per cent. alcohol. They were not taken from their cases when collected. When ready for study, they were removed by pulling them out with a pair of forceps or by splitting the case. They were then dropped into boiling caustic potash to clear and soften. The abdomen was then snipped and the internal parts removed by pressure upon the chitinous parts. The heads were removed and studied separately, drawings being made of the dorsal, ventral and lateral aspects. The details were determined from specimens mounted in balsam. In most cases the whole dorsal and ventral aspects of the head were preserved by splitting the head along the lateral margin from the mandible to the occipital foramen. On one half, the fronto-clypeus, labrum and right mandible were thus held intact, while the gula, labium, maxillæ and left mandible were likewise preserved in position on the other half. Drawings were made with a compound microscope and a camera lucida. The magnification varies, as an attempt was made to have all the drawings of a uniform size.

2. *General Description of the Head:* The head capsule is an elliptical box with two large openings, the occipital foramen and the oral foramen. It is composed of three primary sclerites; a median cephalic fronto-clypeus, a vertex, and a median ventral gula (Plate VI, Figs. 1, 2, 3). The fronto-clypeus is a flat plate bounded on each side by the arms of the epicranial suture, while its cephalic margin is a long transverse border to which the membranous preclypeus is attached. The labrum is joined to the preclypeus. The caudal end of the fronto-clypeus is pointed, fitting into the angle formed by the arms of the epicranial suture. The lateral margins are either straight, regularly curved or sharply indented near their middle. These indentations mark the places of invagination of the pretentoria.

The vertex forms the greater part of the head capsule; it is separated on the dorsal aspect of the head by the fronto-clypeus and on the caudal aspect to the occipital foramen by the stem of the epicranial suture. The vertex extends laterad and ventrad to form the lateral and the greater part of the ventral aspect of the head. In some forms the vertex is contiguous for the greater part of its length on the ventral aspect, being separated only by the gular suture. In other forms, however, it is widely separated by the gula itself (Plate VIII, Fig. 43). In this case the gula extends from the occipital foramen to the proximal end of the labium, but in the former case it is restricted to a small triangle adjacent to the labium. In the first case the vertex alone surrounds the occipital foramen. In the latter case the gula and vertex together bound it. The vertex bears the eyes and the antennæ. The labrum is a subelliptical sclerite which serves as an upper lip. It is generally notched on its free margin. The preclypeus which attaches it to the fronto-clypeus is inserted a short distance cephalad of the posterior edge. The ventral aspect is generally membranous, heavily bristled and continued caudad as the epipharynx.

3. *Mouth-parts:* The mandibles are roughly pyramidal or pyriform. The articulations are of the acetabulum-condyle type. The dorsal articulation has the acetabulum on the mandible and the condyle on the vertex, while in the ventral one the conditions are reversed (Plate VI, Fig. 2). Movements of the mandibles are effected by two tendons which swing them on their articulations like a gate. Flat scissors-shaped and thick chisel-shaped mandibles occur. Their inner surfaces are either toothed for grasping or hollowed out for crushing. The inner basal margins are attached to the lateral membranes of the mouth.

The labium and maxillæ are united and together form an under lip. The labium is median in position and has its basal attachment on the cephalic margin of the gula. Its shape is more or less triangular, broad at the base and terminating in the hemispherical segment, the fused stipulæ. This terminal segment bears a pair of one or two segmented labial palpi, while at its tips, the fused glossæ, is the single opening for the salivary glands.

The maxillæ are generally about the same length as the labium. The basal attachment is by means of the chitinous cardo. The stipes is a small flexible, subcylindrical segment with its mesal margin fusing with the lateral margin of the submentum. Its basal and lateral margins are attached to the cardo, vertex and the inner basal membranes of the mandibles. The stipes is supported by a chitinous cuff that nearly surrounds it. The stipes itself is not capable of much independent movement, but together with the labium, the lower lip moves freely. The terminus of the maxilla is generally composed of two parts, the galea and the maxillary palpus. In some cases they are fused along their adjoining faces to form a single flexible projection which is heavily armored with bristles and supplied with numerous sense organs. The maxillary palpi are either four or five segmented. The segments of these palps are usually not completely chitinized; the chitinization being in the form of a cuff and leaving the mesal surface open to movement. The proximal segment of the maxillary palpus is generally indistinguishable from the proximal end of the galea except for the cuff.

The membranous glossæ are continuous with the parapharynx. The lateral boundaries of the labium are not clearly separated from the maxillæ, especially in the cases where chitinization is slight. The mentum and submentum are likewise not distinguishable. The submentum however generally bears a single large median plate or a pair of small plates.

The eyes generally consist of six simple, closely adjacent, ocelli, placed on a pigmented eye-spot. These eyes are slightly elevated. Their position on the vertex varies from a point near the laterocephalic margins of the head to a point as far caudad as the separation of the epicranial arms.

The antennæ are simple. Siltala recognizes two types: one with two distal pieces, the other with only one. Their position varies with that of the eyes from immediately behind the mandibles to a point far up on the head.

4. *Internal Skeleton:* The endoskeleton of the head is greatly reduced. The tentoria consist of a single pair of flexible fiber-like arms extending through the head from the dorsal to the ventral wall. The dorsal invaginations are found in the indentations of the epicranial arms, while the ventral invaginations are located in the angles formed by the gula and the vertex in the open type and near the caudal ends of the gular suture in the closed type. The supratentoria and corpotentoria are not present in the late larval stages, although I found a single corpotentorium in an early instar of *Mystrophora americanum.*

The above general description is well illustrated by the Phryganeid in Plate VI, Figs. 1, 2, 3 and 4. While there is considerable variation in the structure and arrangement of the various sclerites and appendages, there is a remarkable consistency in the occurrence of the described parts, and in no family are the deviations so marked that the sclerites may not be readily identified.

COMPARATIVE STUDY OF HEAD.

1. *Fronto-clypeus:* This shield-shaped sclerite presents a fascinating study in its variation, for here Nature has escutcheoned the genealogy of the order. The simplest type is found in the straight-sided, roughly pentagonal, head piece of Leptocerid 26720 (Plate VI, Fig. 5). From this simple type three principal changes are evident: (1) the rounding of the pointed end; (2) the flaring at the cephalic margins; (3) the indentations of the lateral margins in association with the pretentoria. These three changes may follow a primary tendency to widen the fronto-clypeus, the resultant ornate character of the epicranial arms being due to the anchoring effect of the pretentoria.

Leptocerid I and Leptocerid III illustrate the initiation of these changes (Plate VI, Figs. 6 and 7), while *Leptocella uwarowii* and *Mystacides sepulchralis* show them emphasized still further (Plate VI, Fig. 9). An unusual development of the cephalic margin is characteristic of Leptocerid II (Plate VI, Fig. 8).

The Molannidæ approximate the Leptoceridæ in the shape of the fronto-clypeus. Except for the anterior margin, which is regularly bowed, *Molanna cinerea* (Plate VI, Fig. 10) is a duplicate of *L. uwarowii*. *Molanna* II is a change in the same direction although marked by a chitinous ridge near the cephalic margin (Plate VI, Fig. 11).

The Phryganeidæ specialize in the development of the cephalic flares of the epicranial arms. The arms curve outward sharply as they approach the clypeal suture until they are nearly parallel with it. Then with a right angle bend they meet the latter, forming a small, squarish, projecting corner (Plate VI, Fig. 1).

The type of fronto-clypeus developed in the Phryganeidæ persists with little modification in the remaining families of eruciform larvæ. It is repeated almost to identity in the Calamoceratidæ, Limnophilidæ, and Sericostomatidæ (Plate VI, Figs., 12–18). The expected exceptions are presented in the Odontoceridæ and in a few genera of the sub-family Brachycentrinæ.

The Odontoceridæ lack the small squarish latero-cephalic corners; the epicranial arms proceeding directly to the clypeal suture without bending outward. The same conditions are found in the Brachycentrinæ mentioned above. The evidence that these two similar conditions were brought about in different ways will be presented in the discussion of the chætotaxy of the head.

It is with interest that we find the same developmental tendencies in the campodeiform and the eruciform groups. The Hydroptilidæ (Plate VII, Fig. 19) very closely resemble the Leptoceridæ, while the Rhyacophilidæ approximate the phryganeid pattern, although in the latter the cephalic part of the sclerite is markedly shorter (Plate VII, Fig. 38).

The Philopotamidæ and the Polycentropidæ show approximately the same type of fronto-clypeus as the Phryganeidæ, except for the cephalic flares. The Philopotamidæ are peculiar in that the cephalic margin of this sclerite is asymmetrically notched (Plate VII, Fig. 23).

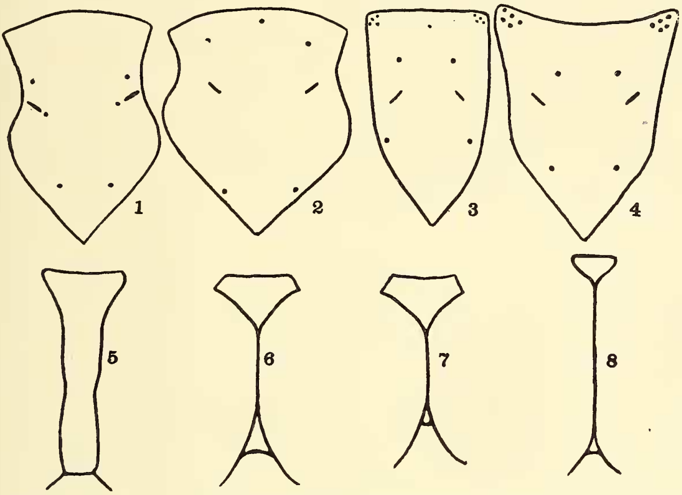
The subfamily Glossosomatinæ depart from the phryganeid pattern in that the epicranial arms take a concave rather than a convex course from the pretentoria to the clypeal suture. This tendency is repeated again in a few hydropsychids and may possibly suggest a relationship.

The Hydropsychidæ of the Eastern United States examined by the author showed a fronto-clypeus which is strikingly different from any other in the order and for a time presented a discontinuous example in an otherwise orderly array. It is roughly triangular and apparently bore no relation to the other types. Through material obtained at Tolon, Colorado, and Soda Butte, Montana, the successive steps in the development of this odd form were made out.

In *Hydropsyche* 27006, the fronto-clypeus is shield-shaped. The lateral margins are formed by a double curve of the epicranial arms, which at first diverge widely, then with a slight curve converge again to points marked by the pretentorinæ. A short outward curve carries them to the convex cephalic margin (text figure 1).

Hydropsyche 27256 has a broader and a longer apex. The epicranial arms do not converge to the degree exhibited by 27006. The resulting sclerite is broad and shield shaped (text figure 2).

In *Hydropsyche incommoda,* the epicranial arms are nearly straight (text figure 3), forming a roughly triangular sclerite which is characteristic of nearly all Hydropsychidæ and the Macronematinæ (text figure 4).



TEXT-FIGURE. 1. Fronto-clypeus of *Hydropsyche* 27006 Ill. St. Lab. Nat. Hist. 2. Fronto-clypeus of *Hydropsyche* 27256 Ill. St. Lab. Nat. Hist. 3. Fronto-clypeus of *Hydropsyche incommoda.* 4. Fronto-clypeus of *Macronema zebratum.* 5. Gula of *Hydropsyche* 27006 Ill. St. Lab. Nat. Hist. 6. Gula of *Hydropsyche* 27256 Ill. St. Lab. Nat. Hist. 7. Gula of *Hydropsyche incommoda.* 8. Gula of *Macronema zebratum.*

Series to demonstrate the simultaneous and correlated development of the dorsal and ventral aspects of the head in the Family Hydropsychidæ.

The three stages given here present a consistent series connecting the aberrant hydropsychid pattern with that of the phryganeid. They indicate the broadening of the sclerite by the shifting of the epicranial arms.

That such a shift has actually taken place is supported by the evidence of the pretentorinæ. In all forms of trichopterous larvæ, except the Hydropsychidæ, the invagination marking the internal skeleton is directly associated with the epicranial arms. In one Molannid the invaginations form a deep depression that lies along the suture (Plate VI, Fig. 11). In *Hydropsyche* 27006 the pretentorinæ are slightly removed from the epicranial arms. In *Hydropsyche* 27256 they are still further removed. In most of the Hydropsychidæ they are displaced to such a distance that one would no longer associate them with the arms.

Thus while the pretentorinæ have retained their original position on the head, the epicranial arms have moved out and away from them, doubtless due to the tendency to broaden the head. In all forms but the Hydropsychidæ, the pretentorinæ have acted as anchoring points and have given the arms their sinuous character. In the Hydropsychidæ the arms have freed themselves and have left the pretentorinæ isolated. We may thus fix the hydropsychid pattern in the phryganeid series.

2. *Chætotaxy of Fronto-clypeus:* A very interesting set of relationships appear with the study of the bristles of the fronto-clypeus. The Leptoceridæ with the straight-sided fronto-clypeus possess only three pairs of bristles (Plate VII, Fig. 28). The first pair, I, are just caudad of the pretentorinæ. The second pair, II, are immediately cephalad, while the third pair, III, are still further removed from the pretentorinæ. The majority of Leptoceridæ have an additional fourth pair, IV, near the cephalo-lateral angles, and a fifth pair, V, slightly laterad to these (*Mystacides sepulchralis,* Leptocerid I, Leptocerid II, Leptocerid III, Leptocerid 13839). *Leptocella uwarowii* presents an additional sixth, VI, between IV and V (Plate VII, Fig. 29).

The Molannidæ show the same three pairs of lateral bristles but with four pairs on the cephalic margin instead of two (Plate VII, Fig. 30). These seven pairs are again present in the Phryganeidæ and the pattern here assumed is repeated with surprising uniformity in the remainder of the eruciform larvæ (Plate VII, Figs. 31–36).

The single median pit is also a noticeable feature of all the eruciform group, with the exception of the Leptoceridæ. This structure has the appearance of a calyx, but I have never found a seta attached at this point.

The few exceptions to typical chætotaxy occur in those forms in which the fronto-clypeus is also exceptional. *Brachycentrus,* lacking the cephalic flares, has only two pairs of bristles on the cephalic margin. The central pit is also absent. This condition suggests relationship with the Leptoceridæ and is further supported by the evidence of the gula. The other exception is *Psilotreta* where but three cephalic pairs were found instead of the typical four (Plate VII, Fig. 35). A fourth pair however were discovered on the vertex in close proximity to the cephalo-lateral corners. The fronto-clypeus in this form is slightly different from the rest of the higher eruciform larvæ. The epicranial sutures proceed directly to the cephalic margins without the little bends that produce the small squarish corners in the sclerite. Were these present they would include this fourth pair of setæ. In no other form of the eruciform larvæ are there any setæ present on the vertex in close proximity to the clypeus at its anterior margin. The fourth pair then in *Psilotreta* is probably represented by this pair displaced on the vertex, and suggests a shift from the phryganeid pattern.

The exact position of the seven pairs of setæ may vary slightly in the several eruciform families or even within a genus, but the general relationship is practically constant.

In the campodeiform group, the same general pattern is present but with a greater diversity in number and arrangement of the setæ. Hydroptilid II shows a clypeus similar in chætotaxy to that of the Leptoceridæ (Plate VII, Fig. 37). In the remaining families some interesting modifications are to be found.

The Rhyacophilidæ show a peculiar tendency to double the bristles I, II, III. Instead of a single bristle as in *Mystrophora americana* there are two (Plate VIII, Fig. 43), one lying directly mesad of the other. Instead of II in its usual place near the pretentorinæ (*P*), a pair of setæ is found on either side. At a first glance, III is absent; or possibly one of the pair in the normal position of II may be III. The interpretation is best given after reference to conditions in closely related material. Setæ IV, V, VI, and VII are in their normal position in the latero-cephalic corners.

Rhyacophila fuscula (Plate VII, Fig. 38): shows a pair of setæ on each side in place of I. Their arrangement, however, is anterior-posterior instead of lateral as in *Mystrophora*. Here again as in *Mystrophora,* we find a pair of setæ where II should be. Seta III is present in its normal position so that the interpretation of the pair is clear.

Setæ IV, V, and VII are in their normal position. VI is found on the vertex as in *Psilotreta.*

Returning to *Mystrophora americana* again, the explanation of the pair of setæ at II is suggested by the condition in *R. fuscula.* A consideration of the shape of the fronto-clypeus in *M. americana* makes this explanation more certain. The lateral margin of this sclerite is concave on the cephalic half and convex on the caudal half. In the majority of Trichoptera the margin is concave on both halves. An examination of the vertex in the proximity of where III should be, brought to light a pair of setæ that would have the position of III if the clypeus were of the normal type.

Other representatives of the Glossosomatinæ and the Rhyacophilinæ show a similar doubling of setæ I, II, and III.

In the Polycentropidæ a somewhat similar condition is met. Seta I is single and varies in position from near the apex in Polycentropid 13942 (Plate VII, Fig. 40) to a point near the pretentorina in *Phylocentropus* sp.? (Plate VII, Fig. 41). Seta II is double and situated about half way between the pretentorina and the cephalic margin. In Polycentropid I, one of the members of the pair is mesad and cephalad to the other. In *Phylocentropus* the one is so far removed from the other that it is nearer III than it is to its fellow.

In *Polycentropus* I (Plate VII, Fig. 21), seta VII is in the corner, while setæ, V, VI and IV form a small triangle half way between the corner and the median line. In *Phylocentropus* setæ VII, V, and VI are in a straight line with IV slightly cephalad.

The chætotaxy of the Philopotamidæ is even more complicated. Seta I is single and located far caudad, while seta II is double. In Philopotamid 26993 (Plate VII, Fig. 23), one member of the pair is directly mesad to the other, forming a straight line across the clypeus. In *Chimarrha* sp? (Plate VII, Fig. 39) one member of the pair is situated directly cephalad of the other, forming a polygon. Seta III is situated far cephalad, is single and is associated with setæ VII, V, VI, and IV. In the last-named species it assumes a position in the latero-cephalic corners, while the four remaining setæ are grouped on an asymmetrical projection in the cephalic margin. Other Philopotamidæ present various similar arrangements. In several species where the clypeus is extremely asymmetrical, the median calyx is wanting.

In the Hydropsychidæ, the setal arrangement is obscured by the presence of a large number of secondary setæ. Setæ I and II alone are distinguishable.

It is thus apparent from a study of the fronto-clypeus that while variation occurs in shape and chætotaxy, they may all be referred to a common type. This plan has its simplest expression in the Leptoceridæ. The eruciform and campodeiform groups can readily be distinguished from one another by their own peculiarities. The eruciform larvæ tend to perfect the phryganeid pattern in both shape and chætotaxy. The campodeiform larvæ lack the regularity of the eruciform larvæ and individual patterns are developed in the separate families.

3. *Gula:* This sclerite gives an even more instructive series than the one previously discussed, for in the family Hydropsychidæ we find evidence that is indisputable in its confirmation of the new genealogy. In many other families are found straggling remnants of this piece, clearly marking the phylogenetic trail.

I have applied the terms open and closed gula respectively to those cases where the gula reaches the occipital foramen; and where the two parts of the vertex are contiguous preventing the gula from reaching the occipital foramen (Plate VIII, Figs. 44 and 49).

The Leptoceridæ show the greatest development of the open type. In Leptocerid II, the gula is a short broad plate that widely separates the vertex (Plate VIII, Fig. 47). In *Leptocella uwarowii* it is a triangular piece (Plate VIII, Fig. 46), while in *Mystacides* it is a large and quadrilateral area (Plate VIII, Fig. 45). In the Œcitinæ is has the appearance of being overdeveloped. Thus in Leptocerid I it is more than half the width of the head. It is roughly elliptical in shape, while the vertex has a tendency to enclose it (Plate VIII, Fig. 44). The same is true in Leptocerid 11561, except that the shape is quadrilateral, while in Leptocerid 26720 it is sub-crescentic (Plate VIII, Fig. 43).

The gula of the Molannidæ is very much like that of *Mystacides.* They are roughly quadrilateral and distinctly of the open type (Plate VIII, Fig. 48).

The Phryganeidæ show a transition from the open to the closed type. Phryganeid II has an open gula. It is long, narrow, and straight at the cephalic end and roundly pointed at the caudal end.

While the vertex almost encloses the gula, it does not meet behind it. But in *Neuronia postica,* the same style of gula is completely enclosed (Plate VI, Fig. 3).

Other intermediate stages from an open to a closed gula are to be found in the Calamoceratidæ. In *Ganeonema americanum* the main part of the gula is restricted to an enclosed triangle but its strongly pointed end fills the gular suture for nearly its entire length (Plate VIII, Fig. 49).

Similar transitional stages are found in the family Limnophilidæ. *Neophylax* sp. has an open T-shaped gula (Plate VIII, Fig. 50). The vertex almost encloses it but does not meet behind it. In Limnophilid 13277 a gula similar to that of *Ganeonema* is present (Plate VIII, Fig. 51). For a further reduction of the gula, the remaining figures of the Limnophilidæ and the Odontoceridæ should be compared. The extreme condition is represented by *Helicopsyche* and *Psilotreta* (Plate VIII, Figs. 52–55).

Another series of a more striking type is found in the family Sericostomatidæ. The subfamily Brachycentrinæ has a widely open gula (Plate VIII, Fig. 57), the Lepidostomatinæ show a peculiar transitional type, while the gula is enclosed, the vertex fails to meet behind it, and a pair of pseudo-sutures follow those between the gula and the pleuræ on either side (Plate VIII, Fig. 59). The Gœrinæ have a small triangular enclosed gula which is but slightly removed from the occipital foramen (Plate VIII, Figs. 56 and 58).

Most descriptions of the campodeiform larvæ limit the gula to a small triangular sclerite at the proximal end of the labium, or in some cases indicate the complete absence of the gula. The present study shows definitely the limits of the gula and the steps by which it has been restricted.

The Hydroptilidæ have a short broad gula at the proximal end of the labium. It is roughly triangular or keel-shaped. There is also a small triangular sclerite at the end of the gular suture in the angle formed by the junction of the two parts of the vertex. The importance of this small sclerite will become apparent in the discussion of the Hydropsychidæ (Plate IX, Fig. 60).

The gula of the Glossomatinæ (*Mystrophora*) is a sclerite similar in shape to that of the Hydroptilidæ. That of the Rhyacophilinæ is rather large and pentagonal. A very small area of cuticle is noticeable at the end of the gular suture in every specimen examined (Plate IX, Fig. 61).

The Polycentropidæ and Philopotamidæ are similar in having a broad, short, triangular gula (Plate IX, Figs. 62 and 63).

Most of the Hydropsychidæ have a gula shaped like that of the Rhyacophilidæ. This family of Trichoptera furnishes the material for the interpretation of the gular reduction. *Hydropsyche* 27006 has a gula which reaches from the labium to the occipital foramen. It is rather broad, with sides nearly straight and parallel, but diverging at the cephalic ends into a wide flare (text fig. 5 and Plate IX, Fig. 65).

Hydropsyche 27256 has a gula consisting of two pieces, such as would be formed from one like 27006 if the vertex came together near its middle, thus cutting it into a cephalic and a caudal half (text fig. 6 and Plate IX, Fig. 66).

Hydropsyche incommoda has a gula which is irregularly pentagonal. At the base of the gular suture is a minute area which represents all that is left of the caudal piece (text fig. 7 and Plate IX, Fig. 67). *Macronema* has a similar piece wedged into the gular suture, while its cephalic part is further reduced to a small triangular piece (text fig. 8 and Plate IX, Fig. 68).

These three steps in the reduction of the gula alone would indicate the direction of evolution within the order. For it is hardly conceivable that the open type could originate through the spontaneous appearance and the gradual enlargement of the sclerite at the base of the gular suture; that this sclerite could fuse with the enclosed triangular piece already present and that the two together form the broad open type.

Furthermore, the development of the ventral and dorsal aspects of the head are fully correlated. When the data already presented on the fronto-clypeus is compared with that of the gula, we find a complete corroboration.

Hydropsyche 27006 has a long open gula; dorsally the pretentorinæ are only slightly removed from the epicranial arms. *Hydropsyche* 27256 has a two-piece gula; the pretentorinæ are further removed. *Hydropsyche incommoda* has only a trace of the caudal piece of the gula left; the pretentorinæ are no longer associated with the epicranial arms. Thus the modifications of the two sides of the head seem to have been simultaneous and orthogenetic in character.

The small piece wedged into the gular suture in some of the Hydroptilidæ and the Rhyacophilidæ suggests a similar development. The caudal ends in the higher eruciform larvæ also support development from the open type.

Additional evidence could be brought forward in the consideration of the metatentorinæ. In the open type they are always found at the edges of the vertex in the angle formed by the latter and the gula. In the closed type, they are always found at the occipital end of the gular suture, thus furnishing landmarks for the homology of the various structures.

4. *Structure and Position of the Antennæ:* Siltala recognizes two types: one, with a distal segment upon which are mounted two separate so-called palps, and numerous sense bristles; the other with but a single so-called palp. The first form is stated to be common to the campodeiform group, while the second is peculiar to the eruciform group. I have found no trace of antennæ in the Rhyacophilinæ, Philopotamidæ, Polycentropidæ and the Hydropsychidæ.

The antennæ of the Hydroptilidæ are very similar to those of the Leptoceridæ, long, cylindrical and slender, with the palp set on a raised base slightly behind the dorsal mandibular articulation. Exceptionally long antennæ are found in the Œcetinæ, in *Mystacides* and in *Leptocella.* The Molannidæ present the same type and location in antennæ.

In the Phryganeidæ, the antennæ are reduced in size, particularly with respect to the terminal segment. Their position is near the base of the mandibles, but in a more lateral position and separated from the pleural condyle by a pseudo-suture. In the Calamoceratidæ, the antennæ are of the phryganeid type, but are completely removed from the cephalic margin to a position half way up on the head. The Limnophilidæ show the same structure and position of the antennæ.

With respect to this character the Sericostomatidæ show again an interesting developmental series. In the Brachycentrinæ the antennæ are at the cephalic margin; in the Lepidostomatinæ they are halfway between the mandibles and the eyes.

The antennæ are important structures in the consideration of family relationships and receive the best interpretation when we consider the Leptoceridæ as the stem form. Otherwise it is difficult to account for the fact that they are well developed in the Hydroptilidæ, lost in one subfamily of the Rhyacophilidæ, and the other families of the campodeiform group, present again in the Leptoceridæ with greatest functional development, and then consistently reduced in size and migrating up the sides of the head in the remaining eruciform larvæ.

Conclusions.

The foregoing pages give a fairly comprehensive description of the head of the trichopterous larvæ. While much detail could be added, those characters of primary importance have been examined and discussed. Before going into the anatomy of the thorax and abdomen, it might be well to sum up the data concerning the head to see if anything like order exists in the relationship of the various parts among the respective families.

The sclerite showing the greatest variation in form is the gula. The two types are the open and the closed. The open type is found primarily in the eruciform group and has its greatest development in the family Leptoceridæ. A graded series of forms is found within the eruciform families which leads from the open to the closed type. The successive steps are from the Leptoceridæ to the Molannidæ, Phryganeidæ, Calomoceratidæ, Limnophilidæ, and the Odontoceridæ. The Sericostomatidæ show a like series within the subfamilies, ranging from an open gula in the Brachycentrinæ to a partially closed one in the Lepidostomatinæ, to a closed one in the Gœrinæ. The closed type is clearly derived from the open. The vertex has come together behind the gula and enclosed it. In some cases the straggling caudal end is still to be seen in the gular suture.

The campodeiform larvæ show, with but few exceptions, the extreme closed type. The method of development of this type is clearly shown in the Hydropsychidæ, where an open gula, a gula constricted into two equal pieces, and a gula constricted into a cephalic part and a minute caudal piece have been demonstrated.

The closed gula of the campodeiform larva is thus brought about by the constriction of the open type into two pieces with the subsequent reduction and disappearance of the caudal piece.

The relationship on the basis of gula would indicate the Leptoceridæ as the stem form, with the higher eruciform larvæ diverging in one direction through the enclosure of the gula by confinement, while the campodeiform larvæ vary in the same direction in the enclosure of the gula by constriction.

A consideration of the fronto-clypeus lends corroborative evidence to the new arrangement of the families of Trichoptera. The straight-sided simpler types are found in the Leptoceridæ. With the pretentorinæ as anchoring points the epicranial arms have bowed above and below to form a sclerite of graceful contour. The development of the various forms is through the Molannidæ, Phryganeidæ to the Limnophilidæ respectively, thus bearing out the family relationships as established for the gula.

The only family in which the epicranial arms have left the pretentorinæ is the Hydropsychidæ. And in this case we find a very definite correlation between the development of the fronto-clypeus and the gula. In the hydropsychid with the open gula, the pretentorinæ are only slightly removed from the epicranial arms; in the species with the gula constricted into two equal halves the pretentorinæ are further removed from the epicranial arms; in the majority of hydropsychids, where the pretentorinæ would not be associated with the epicranial arms, the gula is restricted to a very small triangular piece at the cephalic end of the gular suture.

The chætotaxy of the fronto-clypeus indicates by itself the same general arrangement as that established for the shape of this sclerite and the shape of the gula.

While the labrum shows nothing so definite in its development as do the fronto-clypeus and gula, yet all the positive evidence would favor the new arrangement. It is in the higher campodeiform larvæ that the most highly specialized, asymmetrical labra exist.

The mandibles also have undergone little change. Two types, however, are distinct. The thin, flat, knife-shaped type is characteristic of the Leptoceridæ, Molannidæ, Phryganeidæ and most of the campodeiform larvæ. The thick, blunt, chisel-shaped type is found in the eruciform larvæ.

The labium, while it has undergone little change in special development, shows a consistent and verifying plan in the chitinization of the submentum. The two bristles, constantly present, leave no doubt as to the identity of the plate. From a condition of no chitinization in the Leptoceridæ to one in which small plates are laid down at the base of the setæ in the higher eruciform, further chitinization produces a large single median plate in the campodeiform larvæ. This reaches its highest development in the bilobed plate in the Hydropsychidæ.

The maxillæ, while giving little in the way of positive evidence, present no difficulties for the new arrangement of trichopterous genealogy. The maxillary palpi are five-segmented throughout with the exception of the Leptoceridæ. The latter, together with the campodeiform larvæ, possess long slender, flexible, maxillary palpi, while those of the eruciform larvæ are short, blunt and heavily chitinized.

The position of the eye supports the new arrangement. The eyes are far cephalad in the Leptoceridæ. The movement in the eruciform larvæ is away from, while in the campodeiform larvæ it is towards, the cephalic margin of the head. This is doubtless correlated with the respective attitudes of the head in the two groups.

The position of the antennæ lends further evidence of the same kind. In the Leptoceridæ they are in a cephalic position, gradually retreating caudad on the head, a movement doubtless correlated with the migration of the eyes in the higher eruciform larvæ. When present in the campodeiform larvæ they are far cephalad. The position of the antennæ becomes of primary importance when their origin is considered. They arise as appendages of the premandibular segment. In their embryological development, the earlier stages are adjacent to the bases of the mandibles. This would indicate a generalized condition, while that away from the mandible would be specialized. The embryological studies of Patten on *Neophylax,* a Limnophilid, show the migration of the antennæ from a cephalic to a lateral position.

All these data taken together favor the assumption that the Leptoceridæ are the stem form, with two principal lines of development, the eruciform and the campodeiform types. The Hydroptilidæ are a very early offshoot and not directly related to the campodeiform type with which they are ordinarily associated.

If this hypothesis be correct, we should expect to find some degree of correlation in the development of the structures of the thorax and the abdomen. This study has been made and the author hopes to publish the results in a subsequent paper.

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EXPLANATION OF PLATES.

PLATE VI.

FIG. 1. *Neuronia postica,* dorsal aspect of the head. *L,* labrum; *Md,* mandible; *LM,* labral membrane; *FC,* fronto-clypeus; *Pl,* vertex; *EA,* epicranial arms; *Pt,* pretentorina; *E,* eye; *A,* antennæ.

FIG. 2. *Neuronia postica,* lateral aspect of head. *Pl,* vertex; *T,* tentorium; *Mx,* maxilla; *Li,* labium.

FIG. 3. *Neuronia postica,* ventral aspect of the head. *Pl,* vertex; *OF,* occipital foramen; *M,* metatentorina; *G,* gula; *Li,* labium.

FIG. 4. *Neuronia postica,* ventral aspect of the labium and maxilla. *G,* gula; *Sm,* sub-mentum; *M,* mentum; *Gl,* glossæ; *Pl,* labial palpus; *C,* cardo; *S,* stipes; *La,* lacina; *PM,* maxillary palpus.

FIG. 5. Leptocerid 26720 (Ill. St. Lab.). Dorsal aspect of head.

FIG. 6. Leptocerid I (Cold Spring Harbor). Dorsal aspect of head.

FIG. 7. Leptocerid III (Cold Spring Harbor). Dorsal aspect of head.

FIG. 8. Leptocerid II (Cold Spring Harbor). Dorsal aspect of head.

FIG. 9. *Mystacides sepulchralis* Walk. Dorsal aspect of head.

FIG. 10. *Molanna cinerea* Hag. Dorsal aspect of head.

FIG. 11. *Molanna* II (Cold Spring Harbor). Dorsal aspect of head.

FIG. 12. *Ganonema americanum* Walk. Dorsal aspect of head.

FIG. 13. *Stenophylax luculentus.* Dorsal aspect of head.

FIG. 14. *Neophylax* sp. Dorsal aspect of head.

FIG. 15. *Psilotreta frontalis* Banks. Dorsal aspect of head.

FIG. 16. Lepidostomatid I (Cold Spring Harbor). Dorsal aspect of head.

FIG. 17. *Gœra* sp.? Dorsal aspect of head.

FIG. 18. *Brachycentrus nigrisoma* Banks. Dorsal aspect of head.

PLATE VII.

FIG. 19. Hydroptilid II (Cold Spring Harbor, N. Y.). Dorsal aspect of the head.

FIG. 20. *Rhyacophila fuscula* Walk.

FIG. 21. Polycentropid I (Cold Spring Harbor).
FIG. 22. *Phylocentropus* sp.
FIG. 23. Philopotamid 26993 (Ill. St. Lab.).
FIG. 24. Hydropsychid 27006 (Ill. St. Lab.).
FIG. 25. Hydropsychid 27256 (Ill. St. Lab.).
FIG. 26. *Macronema zebratum* Hag.
FIG. 27. *Hydropsyche incommoda.*
FIG. 28. Leptocerid 29451 (Ill. St. Lab.). Enlarged view of the fronto-clypeus to show the details of chætotaxy.
FIG. 29. *Leptocella uwarowii* Kol.
FIG. 30. *Molanna cinerea* Hag.
FIG. 31. Phryganid sp.
FIG. 32. *Ganonema americanum* Walk.
FIG. 33. Lepidostomatid I (Cold Spring Harbor).
FIG. 34. *Anabolia* sp.
FIG. 35. *Psilotreta frontalis* Banks.
FIG. 36. *Brachycentrus* sp. (Cold Spring Harbor).
FIG. 37. Hydroptilid II (Cold Spring Harbor).
FIG. 38. *Rhyacophila fuscula* Walk.
FIG. 39. *Chimarrha* sp. Ithaca.
FIG. 40. Polycentropid 13942 (Ill. St. Lab.).
FIG. 41. *Phylocentropus* sp.
FIG. 42. *Mystrophora americana* Banks.

PLATE VIII.

FIG. 43. Leptocerid 11561 (Ill. St. Lab.). Ventral aspect of the head.
FIG. 44. Leptocerid I (Cold Spring Harbor).
FIG. 45. *Mystacides sepulchralis* Walk.
FIG. 46. *Leptocella uwarowii* Kol.
FIG. 47. Leptocerid II (Cold Spring Harbor).
FIG. 48. *Molanna cinerea* Hagen.
FIG. 49. *Ganonema americanum* Walk.
FIG. 50. *Neophylax* sp.
FIG. 51. Limnophylid 13277 (Ill. St. Lab.).
FIG. 52. *Anabolia bimaculata.*
FIG. 53. *Helicopsyche borealis.*
FIG. 54. *Stenophylax* sp.
FIG. 55. *Psilotreta frontalis* Banks.
FIG. 56. *Gœra pilosa* Fab.
FIG. 57. *Brachycentrus nigrosoma* Banks.
FIG. 58. *Limnephilus indivisus.*
FIG. 59. *Lepidostoma* sp.

PLATE IX.

FIG. 60. Hydroptilid II (Cold Spring Harbor). Ventral aspect of the head.

FIG. 61. *Rhyacophila fuscula* Walk.

FIG. 62. Polycentropid 13942 (Ill. St. Lab.).

FIG. 63. *Chimarrha* sp. (Ithaca).

FIG. 64. *Mystrophora americana* Banks.

FIG. 65. Hydropsychid 27006 (Ill. St. Lab.).

FIG. 66. Hydropsychid 27256 (Ill. St. Lab.).

FIG. 67. *Hydropsyche incommoda.*

FIG. 68. *Macronema zebratum* Hag.

FIG. 69. Leptocerid I (Cold Spring Harbor). Ventral aspect of the labium and maxilla.

FIG. 70. *Leptocella uwarowii* Kol.

FIG. 71. *Molanna cinerea* Hag.

FIG. 72. *Ganeonema americanum* Walk.

FIG. 73. *Psilotreta frontalis* Banks.

FIG. 74. *Brachycentrus nigrosoma* Banks.

FIG. 75. *Arctœcia medialis* Banks.

FIG. 76. Hydroptilid I (Cold Spring Harbor).

FIG. 77. Rhyacophilid I. Tolon, Colo.

FIG. 78. Philopotamid 26993 (Ill. St. Lab.).

FIG. 79. *Mystrophora americana* Banks.

FIG. 80. *Phylocentropus* sp.

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A NEW WALKING-STICK INSECT FROM EASTERN NORTH AMERICA.

By WM. T. DAVIS,

STATEN ISLAND, N. Y.

In the low-lying meadows, and occasionally elsewhere on Staten Island, Long Island, as well as in other localities along the Atlantic coast, there is a walking-stick insect to be found on the golden-rods and associated plants that has interested entomologists for some time. It has passed under the name of *Manomera blatchleyi* (Caudell), but as no males have been recorded, much uncertainty has existed regarding the specific name.

Bacunculus blatchleyi Caudell was described in the JOURNAL, New York Entomological Society, Vol. 13, p. 212, 1905, from a male collected in Starke County, Indiana, and according to Mr. Blatchley in